

## CHROMOSOMES OF MEXICAN SEDUM II. SECTION PACHYSEDUM

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This is the second of several papers reporting altogether the chromosomes of about 90 species of Mexican *Sedum*. A general introduction, materials and methods, and acknowledgements are included in the first paper (Uhl, 1976b).

Berger (1930) proposed sect. *Pachysedum* to include those shrubby and subshrubby Mexican species of *Sedum* that have thickened, terete or subterete leaves. He also proposed sects. *Dendrosedum*, *Fruticisedum*, and *Leptosedum* to include certain other, mostly large, Mexican species, some of which resemble sect. *Pachysedum*. Clausen (1943) considered that Berger's four sections plus his own new sect. *Craigia* warranted status as subg. *Pachysedum* (Berger) Clausen. In the most recent general treatment, Jacobsen (1974) followed Berger closely, adding some more recently described species and sect. *Centripetalia* Alexander.

However, Walther (1931) was more impressed with the lateral inflorescences of many of these species, and he proposed sect. *Bergerosedum* to include those species of Berger's sects. *Pachysedum* and *Dendrosedum* having this character. (In doing so he excluded *Sedum cremnophila* and *S. corynephyllum*, which have lateral inflorescences and which Berger had included in his sect. *Pachysedum*, and he inadvertently included two species whose floral stems are not truly lateral.) The evidence from cytology presented here and also the evidence obtained from many artificially produced hybrids (Uhl, 1976a, and unpublished) indicates that the mostly large and thick-leaved species with lateral inflorescences, or at least most of them, form a natural group, referred to here as sect. *Pachysedum*. All of these species have  $n = 30$  to  $n = 36$  or a multiple (except for  $n = 26$  in *S. hultenii*). Most of them can be intercrossed readily in cultivation, and the resulting hybrids exhibit mostly bivalent chromosome pairing at meiosis, which indicates that their genomes are organized in very similar ways (Uhl, 1976a, and unpublished). The same kind of evidence also indicates that species of sect. *Pachysedum* are less closely related to other species of *Sedum* having terminal inflorescences.

Of the species listed under sect. *Pachysedum* by Jacobsen (1974), *Sedum eichlamii* is a horticultural name without taxonomic standing, and *S. guatemalense* Hemsley and *S. morganianum* Walther are excluded from the present treatment because of their terminal inflorescences. On the other hand, *S. confusum* Hemsley, including its synonym *S. aoikon* Ulrich (Clausen, 1975), and *S. dendroideum* DC of Jacobsen's sect. *Dendrosedum* and *S. cuspidatum* Alexander and *S. hultenii* Fröderström of his sect. *Frutisedum* are included with sect. *Pachysedum* here because of their lateral inflorescences and for other reasons. The recently named *S. batallae* Barocio (1973), *S. clavatum* Clausen (1975), *S. decumbens* Clausen (1975), *S. macdougallii* Moran (1977), possibly *S. suaveolens* Kimnach (1978), and one species as yet unnamed also are considered to belong to sect. *Pachysedum* and are reported here.

This paper reports numbers of 82 collections, representing all 19 species here considered to constitute sect. *Pachysedum*, modified as indicated from Jacobsen (1974), and including sect. *Craigia* Clausen. Three additional named species are reported here because they are considered to be natural or garden hybrids each probably having a species of sect. *Pachysedum* as one parent.

Four of the 19 species treated here, *Sedum corynephyllum*, *S. craigii*, the new *S. suaveolens*, and the unnamed UC58.858, have corollas that are anomalous for *Sedum*: erect in the lower half or more, instead of spreading from the base as in the other 15 species of sect. *Pachysedum* and in typical species of *Sedum*. In this character they resemble members of subfam. Echeverioideae, but they do not fit well into any genera of that subfamily. Jacobsen (1974) assigned *S. corynephyllum* and *S. craigii* to his sect. *Pachysedum*, and their subshrubby habit, very thick leaves, lateral inflorescences, and basic chromosome numbers ( $x = 30-34$ ) are all compatible with this treatment. The same situation applies also to the undescribed UC58.858. Furthermore, in certain hybrids the chromosomes of *S. corynephyllum* and UC58.858, at least, have a very high degree of homology with those of certain other species of sect. *Pachysedum*, as shown by very extensive chromosome pairing (Uhl, unpublished). (*Sedum craigii* flowers at a different season from all the other species, and this has limited opportunities for hybridizing.) Details of the hybrids involving species of sect. *Pachysedum* will be published separately, but a few hybrids of special interest are mentioned below in the accounts of their parental species.

Although vegetatively of very different aspect from other species of sect. *Pachysedum*, the recently discovered and named *Sedum suaveolens* is included in this treatment because of similarity of its flowers to those of *S. craigii* (Kimnach, 1978).

#### SPECIES

##### ***Sedum adolphii*, *Sedum nussbaumerianum*.**

*Sedum adolphi* Hamet and *S. nussbaumerianum* Bitter are very similar and possibly conspecific (Clausen, 1959). All plants studied cytologically came from cultivation, where both species are widespread. No field locality has been reported for *S. adolphii*, and Clausen (1959) was unable to find *S. nussbaumerianum* in the large barranca which is its type (and only) locality. Plants discovered this year by Felipe Otero and by myself in two locations at low elevations in the state of Veracruz have not been studied cytologically as yet. In terms of the basic chromosome numbers of the section ( $x = 30-36$ ), both species are tetraploid ( $n = 64$ ), and most plates at metaphase I include some apparent multivalents, which makes exact counts very difficult (Figures 1 & 21). In hybrids most or all of the chromosomes of polyploid parents belonging to other genera of the Mexican Crassulaceae pair among themselves, indicating that they are autopolyploids (Uhl, 1970, and unpublished; Uhl & Moran, 1973). It is likely that the same is true also for these and other polyploids of sect. *Pachysedum*, but direct evidence from chromosome pairing in their hybrids is not yet available.

##### ***Sedum* × *amecamecanum*.**

*Sedum* × *amecamecanum* Praeger, according to Clausen (1959), is probably a natural hybrid between *Villadia batesii* and *Sedum dendroideum* ssp. *monticola* (later renamed *S. praealtum* ssp. *monticola*, Clausen, 1975). It is morphologically intermediate between the two parents, and Clausen found it only where they occur together. I have noted both terminal and axillary inflorescences, as might be expected in such a hybrid. Clausen also reported that in nature most anthers of *S. amecamecanum* are undeveloped, that in cultivation many pollen grains are small and undeveloped, and that ovules do not develop into seed. No chromosome count is available for *S. praealtum* ssp. *monticola*, but the other two subspecies of *S. praealtum* have  $n = 34-36$  (see below); *Villadia batesii* has  $n = 25$ , and its hybrid with subspecies *monticola* might be expected to have about 60 somatic chromosomes.

The cytological evidence reported here strongly supports the conclusion that *Sedum amecamecanum* is a hybrid, probably of the parentage suggested. Meiosis was highly irregular in both collections studied, with univalents on and off the plate at metaphase I (Figure 2), with many laggards and occasionally a bridge at anaphase I (Figure 3) and sometimes restitution nuclei after meiosis I, and with most quartets including extra spores and/or spores of different sizes after meiosis II (Figure 5).

The two collections studied are not identical. *U483* has pale yellowish flowers and fewer chromosomes, with about 57 univalents counted in one cell. An average of about 15 bivalents and multivalents is estimated for most of its cells at metaphase I, plus a large number of univalents (usually 20 or more), and with 25–32 elements counted on metaphase II plates. This may well be an  $F_1$  hybrid. *M7800*, said to have originated at 3000 meters on Popocatepetl, has white flowers and more chromosomes, usually with 55–57 elements of all kinds at metaphase I and 40–46 elements on each plate at metaphase II (Figure 4). This may be a triploid hybrid, with two sets of chromosomes from *Villadia batesii*: either an  $F_1$  hybrid which received an unreduced gamete from *V. batesii*, or the result of a backcross of an unreduced gamete of the  $F_1$  hybrid to *V. batesii*. Although Clausen (1959) studied different plants from those reported here, he also noted two variants of *Sedum amecamecanum* and concluded on morphological grounds that one may be an  $F_1$  hybrid and the other “the result of a single backcross to *V. batesii*”. He also reported subspecies *monticola* only from Iztaccihuatl and subspecies *parvifolium* from Popocatepetl. Therefore, *S. amecamecanum* from Popocatepetl—if the locality data for *M7800* are correct—might result from *V. batesii* crossed there with *S. praealtum* ssp. *parvifolium*.

#### ***Sedum batallae*.**

*Sedum batallae* Barocio ( $n = 34$ , Figure 6) is known only from a few square meters on a sheer cliff in southern Hidalgo. In describing this species, Barocio (1973) considered that it shows some similarity to *S. compactum* ( $n = 58$ ) of Fröderström's (1935) group *Minimum*. However, its lateral inflorescence, its thickened leaves, and its chromosome number suggest that it is a diminutive member of sect. *Pachysedum*. Furthermore, like larger sect. *Pachysedum* species, it is easily hybridized with species of subfam. Echeverioideae, and

extensive chromosome pairing occurs in these hybrids (7 analyzed, Uhl, 1976a, and unpublished).

#### **Sedum clavatum.**

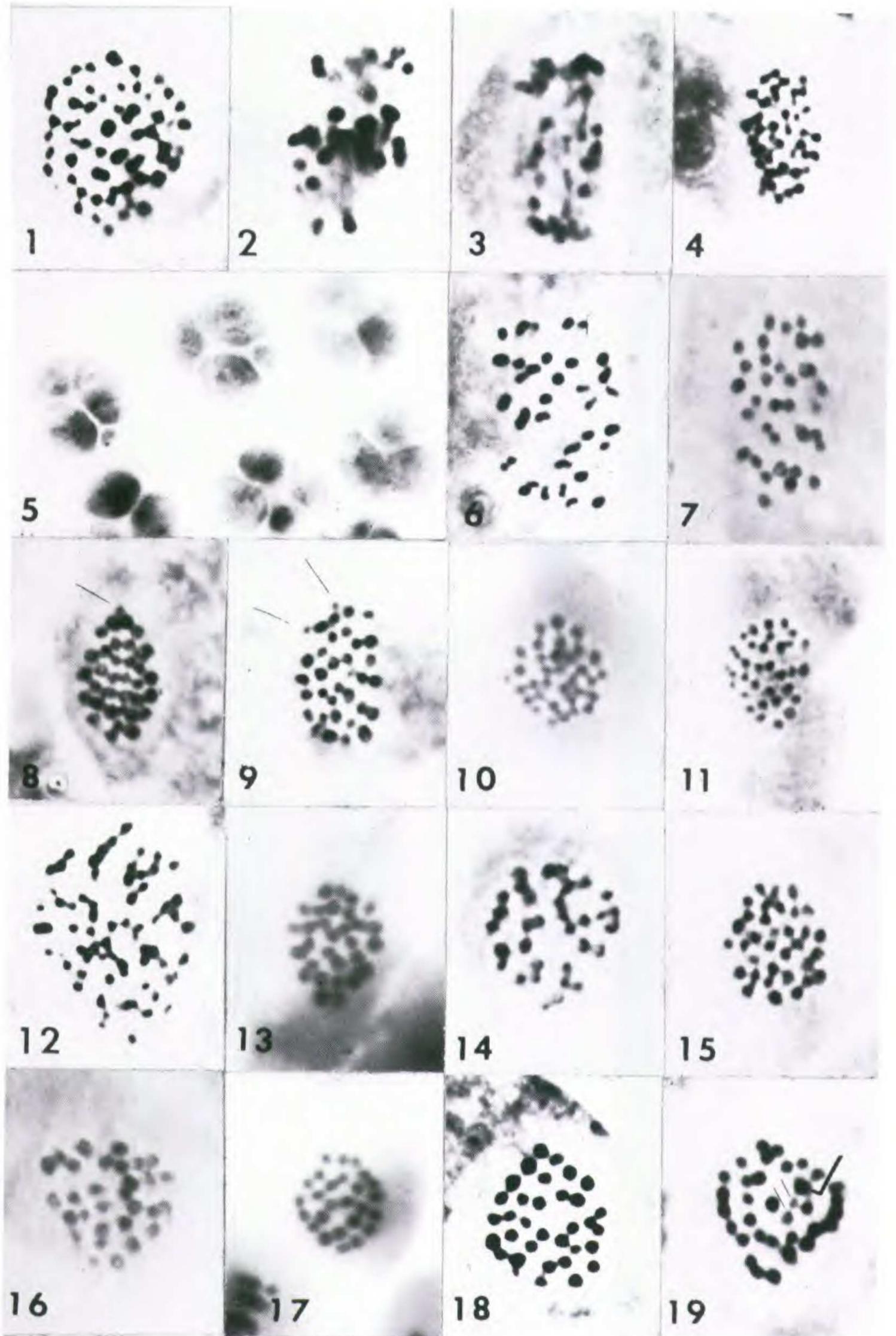
*Sedum clavatum* Clausen (1975) ( $n = 33$ ) is only recently named, although it was earlier described in detail as the "*Sedum* of the Tiscalatengo Gorge" (Clausen, 1959). It is known only from one locality, a canyon southeast of the Nevado de Toluca in the southern part of the state of Mexico, and probably all three collections came from the same population. The type clone (*TMV-T-Tis 1*) has a small extra (B-) chromosome, and some of its cells at anaphase I show a chromosome bridge, but another plant of the type collection (*TMV-T-Tis 3*, Figure 7) has no B-chromosomes or bridges. One B-chromosome also was noted in one of the other collections (*M19058*, Figure 8), and two in the third (*U1566*, Figure 9). Clausen (1975) considered the species to be closest to *S. lucidum* but did not assign it to a section.

#### **Sedum confusum, Sedum decumbens.**

*Sedum confusum* Hemsley ( $n = 34$ , Figure 10) was earlier described in detail by Clausen (1959) as *S. aoikon*, which he now considers to be a synonym (Clausen, 1975). It resembles the common *S. praealtum* ( $n = 34, 35, 36$ ) but is smaller. Long known only in cultivation, it has recently been reported from northern Puebla (Clausen, 1975). The newly described *S. decumbens* Clausen ( $n = 34$ ) also is similar, but smaller still and of unknown origin in the wild.

#### **Sedum corynephyllum.**

*Sedum corynephyllum* Fröderström ( $n = 34, 68$ ) was first described as a monotypic genus, *Corynephyllum viride* Rose. This treatment has generally not been accepted (e.g., Berger, 1930; Fröderström, 1935), and Jacobsen (1974) lists the species in his sect. *Pachysedum* as *S. viride* (Rose) Berger (a name preëmpted by the earlier *S. viride* Makino). The collections studied all came from the Atlantic slope of the Sierra Madre Oriental, from southern San Luis Potosi southeast for nearly 200 km into eastern Hidalgo. The three tetraploid collections ( $n = 68$ , Figure 12) all came from the Barranca de Metztitlan, Hidalgo, in the southeastern part of the range and possibly all from the same population. All collections from farther north and west were diploid ( $n = 34$ , Figure 11).



***Sedum craigii*.**

*Sedum craigii* Clausen ( $n = 30$ , Figure 13) until recently was the only *Pachysedum* known to be native to western Mexico, and it is the only species that usually flowers in the fall. Apparently only one plant, thought at first to be *Graptopetalum amethystinum*, has ever been collected (Lindsay, 1943), and both collections reported here probably had the same origin (rim of Barranca del Cobre, in western Chihuahua). In describing this species, Clausen (1943) commented on its unusual combination of characters, especially its erect but separate petals, recurved at the tips. However, he felt that it "seemed as near to *Sedum*" as to any other genus, and he assigned it to a new section, *Craigia*, of his subg. *Pachysedum*. Jacobsen (1974) did not accept Clausen's section and listed *S. craigii* with sect. *Pachysedum*.

*Sedum craigii* differs in its chromosome number ( $n = 30$ ) from all other species of sect. *Pachysedum* except *S. dendroideum*, which does not seem particularly close to it morphologically. A surprisingly close relative is *Echeveria affinis*, also  $n = 30$ , also native to western Mexico, and which also flowers during the fall, when few other Mexican Crassulaceae are in bloom. A hybrid between these two species shows completely bivalent chromosome pairing in nearly every cell, produces 17.7% stainable pollen, and appears to be slightly fertile (Uhl, unpublished). Also similar to *S. craigii* in floral structure (but not in vegetative aspect) is the anomalous new *S. suaveolens* (Kimnach, 1978).

***Sedum cremnophila*.**

*Sedum cremnophila* Clausen (*Cremnophila nutans* Rose) ( $n = 33$ , Figure 14) is known only from cliffs within a few kilometers north and south of Tepoztlan, Morelos. It has all of the morphological

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Figures 1–19. Chromosomes of *Sedum* sect. *Pachysedum* at metaphase I in pollen mother cells,  $\times 2000$  (except as indicated). Thin lines point to univalents or B-chromosomes, thicker lines to multivalents. 1, *S. adolphii*, C45–97,  $n = 64$ ; 2–5, *S.  $\times$  amecamecanum*: 2, U483, spindle view, with univalents off the metaphase I plate; 3, U483, lagging univalents at anaphase I; 4, M7800, 42 elements at metaphase II; 5, U483, abnormal quartets with undersized microspores,  $\times 800$ ; 6, *S. batallae*, M13411,  $n = 34$ ; 7–9, *S. clavatum*: 7, TMV-T-Tis 3,  $n = 33$ ; 8, M19058,  $n = 33 + 1B$ ; 9, U1566,  $n = 33 + 2B$ ; 10, *S. confusum*, C44–14,  $n = 34$ ; 11–12, *S. corynephyllum*; 11, U258,  $n = 34$ ; 12, M7796,  $n = 68$ ; 13, *S. craigii*, C43–2,  $n = 30$ ; 14, *S. cremnophila*, M10174,  $n = 33$ ; 15, *S. cuspidatum*, U1263,  $n = 34$ ; 16, *S. dendroideum*, M7779,  $n = 30$ ; 17, *S. hultenii*, C7472,  $n = 26$ ; 18, *S. lucidum*, C44–12,  $n = 34$ ; 19, *S.  $\times$  luteoviride*, M7801, 31 bivalents, 1 trivalent, and 2 univalents.

and cytological characteristics of sect. *Pachysedum*, and hybrids with three other species of sect. *Pachysedum* (*S. batallae*, *S. cuspidatum*, *S. lucidum*, and *S. praealtum*, all having  $n = 34$ ) show almost completely bivalent chromosome pairing, indicating close homology (Uhl, 1976a). *Sedum cremnophila* is also very similar vegetatively to *Echeveria linguifolia*, which also has  $n = 33$ , and these two species have been crossed reciprocally in cultivation to give fertile hybrids with normal meiosis (Uhl, 1976a). The  $F_1$  hybrids have been back-crossed in various combinations to both parents to give second-generation progeny which also have apparently normal meiosis. Clearly *Sedum cremnophila* and *Echeveria linguifolia* are very closely related, and their traditional classification into the type genera of different subfamilies does not correspond to their natural relationship. Hybrids of *Echeveria linguifolia* with three other species of sect. *Pachysedum* (*S. batallae*, *S. cuspidatum*, and the undescribed UC58.858, all with  $n = 34$ ) also show mostly bivalent chromosome pairing (Uhl, 1976a), adding strong additional evidence for close relationship of *Echeveria linguifolia* with sect. *Pachysedum*.

Considering the similarity in their morphology and in their chromosomes, Moran (1978) has proposed to revive the genus *Cremnophila* Rose for *Sedum cremnophila* and *Echeveria linguifolia*. However, the chromosomes of both of these species are so closely homologous also with the chromosomes of various other species of sect. *Pachysedum* (Uhl, 1976a) that it seems desirable to keep them all together taxonomically, either as sect. *Pachysedum* of *Sedum* or possibly as a separate genus, *Cremnophila*.

#### ***Sedum cuspidatum*.**

*Sedum cuspidatum* Alexander ( $n = 34$ , Figure 15) originated from two localities about 125 km. apart in eastern Oaxaca and western Chiapas. A greenhouse hybrid with *S. cremnophila* is partly fertile and served as seed parent of a second-generation hybrid having as pollen parent the  $F_1$  hybrid *S. cremnophila*  $\times$  *E. linguifolia* (Uhl, 1976a). The second-generation hybrid shows nearly normal meiosis, produces 59% stainable pollen, and may itself be fertile. Hybrids of *S. cuspidatum* with *S. lucidum* ( $n = 34$ ) and with *S. treleasei* ( $n = 34$ ) also show essentially normal meiosis, with 34 bivalents in nearly all cells, but neither of these hybrids is fertile.

**Sedum dendroideum.**

*Sedum dendroideum* DC (sensu strictu) differs in its chromosome number ( $n = 30$ , Figure 16) from the similar *S. praealtum* ( $n = 34, 35, 36$ , Figures 23, 24, 25), formerly included under it (Clausen, 1959), and from the smaller *S. confusum* and *S. decumbens* (both  $n = 34$ ). Clausen (1959) considered the species to be native only to the Sierra Madre del Sur and to Guatemala, but apparently some populations occur considerably farther north. The five plants reported here came from Hidalgo to eastern Oaxaca, a distance of more than 600 kilometers, and I have a collection (that has not flowered) from the state of Mexico. Both *S. dendroideum* and *S. praealtum* are reputed to have medicinal value (Clausen, 1959), and possibly their original distributions have been extended by man.

**Sedum hultenii.**

*Sedum hultenii* Fröderström consistently has  $n = 26$  (9 collections, Figure 17). The plants studied came from an area of the Sierra Madre Oriental extending from northern Hidalgo more than 200 km. southeastward into northern Puebla. One collection (U485) received in 1957 from Uppsala, Sweden, may have originated from Fröderström's type collection of 1932, which he reported (1935) as being in cultivation in Sweden.

*Sedum hultenii* has lateral inflorescences and in vegetative appearance it seems to lie at the end of a morphological series: *S. dendroideum* — *S. praealtum* — *S. confusum* — *S. decumbens* — *S. hultenii*. It is included here with sect. *Pachysedum*, but its chromosome number ( $n = 26$ ) is anomalous, and it may not be closely related to the other species of the section. Most other species of sect. *Pachysedum* hybridize readily with each other and with most Echeverioideae, but only one of 22 attempts at crossing *S. hultenii* with 10 of these species has resulted in progeny (with *S. cremnophila*, U1881 × M10174).

**Sedum lucidum.**

*Sedum lucidum* Clausen ( $n = 34$ , Figure 18) is known only from a small area in the Rio Blanco valley, south of the peak of Orizaba, state of Veracruz. Clausen (1959) considered it closest to *S. dendroideum* ( $n = 30$ ) and *S. clavatum* ( $n = 33$ ). It must also be closely related to *S. cuspidatum* ( $n = 34$ ) and to *S. treleasei* ( $n = 34$ ),

for hybrids with those species (*U1263* × *U1462* and *O-RB6* × *U1205*, respectively) show essentially normal meiosis and produce 10.3% and 19.5% stainable pollen.

#### ***Sedum* × *luteoviride*.**

*Sedum* × *luteoviride* Clausen appears to be a natural hybrid. Clausen (1948) originally assigned this species to subg. *Pachysedum*, and Jacobsen (1974) included it with his sect. *Pachysedum*. However, Clausen later (1975) transferred it to subg. *Sedum*. Meiosis was irregular in all five collections studied, and many abnormal microspores are produced. The species was described from cultivated material, with no locality then known for it in the wild (Clausen, 1959). In 1959, near San Vicente, Hidalgo, Dr. Reid Moran and Myron Kimnach found a single plant of *S.* × *luteoviride* (*M7808*) with *S. praealtum* ssp. *parvifolium* (*M7806*,  $n = 35$ ) and *S. greggii* (*M7807*,  $n = 33$ ), and these may be its parents.

Although the total chromosome number appears to be about the same in all collections studied, the amount of pairing at metaphase I differs. The greatest amount of chromosome pairing was noted in *M7801*, where 28–33 bivalents and multivalents (average 30.8) plus 1–10 univalents (average 4.3) were noted in 26 cells analyzed at metaphase I (32 + 2 in Figure 19). Anaphase I has several laggards and occasionally a bridge or two, and one or more chromosomes are sometimes left out of the principal nuclei at telophase I. Most quartets include small extra microspores. By contrast, slides made in two different years of *M7808* (which was collected in the wild) show only 10–26 paired chromosomal elements at metaphase I (average 16.8) plus 15–46 univalents (average 31.6) in 14 cells for which approximate analyses could be made. About 5% of the pollen grains of this plant stained in aniline blue-lactophenol, including many that were abnormal in size.

The morphology of *Sedum luteoviride* and the number and irregular behavior of its chromosomes at meiosis are compatible with its origin as a hybrid between *S. praealtum* of sect. *Pachysedum* and the diminutive *S. greggii*, which has a terminal flowering stem. A vigorous specimen of *M7808* produced both terminal and lateral inflorescences in cultivation. Plants of *M7801* are smaller and produce smaller leaves than *M7808*. Populations of both *S. praealtum* and *S. greggii* differ somewhat in morphology and in chromosome number, and it is likely that *M7801* and *M7808*

resulted from crosses involving different subspecies and/or chromosome races of the two species. A recent attempt to hybridize the two species (*U1187* × *M7807*) has resulted in seven seeds, just planted.

***Sedum macdougallii*.**

*Sedum macdougallii* Moran ( $n = 34$ , Figure 20), only recently named, appears most similar to *S. treleasei* (Moran, 1977). It is known only from its type locality, northeast of Tehuantepec in eastern Oaxaca.

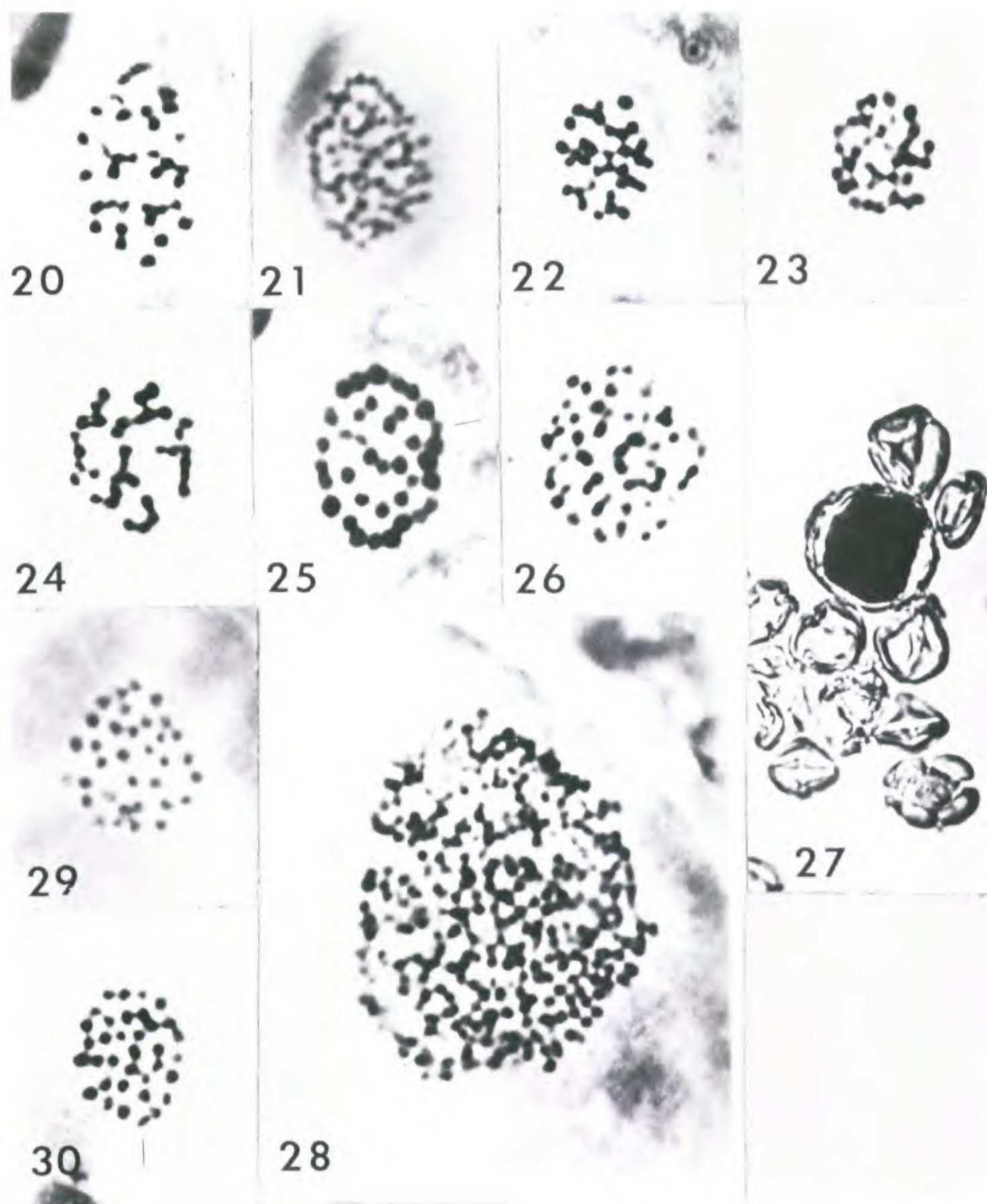
***Sedum pachyphyllum*.**

*Sedum pachyphyllum* Rose ( $n = 34$ , Figure 22) has been studied only from cultivated material of unknown origin in the wild. The species is native to the Sierra Mixteca of northwestern Oaxaca.

***Sedum praealtum*.**

*Sedum praealtum* DC was previously treated as one of four subspecies under *S. dendroideum* (Clausen, 1959). However, Clausen (1975) has recently restricted *S. dendroideum* to include only the one of its former subspecies that has marginal leaf glands and he has reinstated *S. praealtum* to include the other three subspecies. This treatment accords better with the cytological evidence, which shows *S. dendroideum* (sensu strictu) with consistently  $n = 30$  (5 collections, Figure 16), whereas *S. praealtum* ssp. *praealtum* has  $n = 34$  (2 collections, Figure 23) and ssp. *parvifolium* has  $n = 34$  (9 collections),  $n = 35$  (4 collections, Figure 24) and  $n = 36$  (1 collection, Figure 25).

*Sedum praealtum* and the similar *S. dendroideum* are widely cultivated, perhaps because of their reputed medicinal value (Clausen, 1959), and this makes their native distribution difficult to establish. The collections studied here exhibit much more overlap in their distributions than previously indicated (Clausen, 1959). Furthermore, the subspecies of *S. praealtum* apparently intergrade, and some collections are not easily assigned to them. Subspecies *praealtum* ( $n = 34$ ) is probably native in the Rio Blanco valley of Veracruz (Clausen, 1959) and possibly elsewhere. Subspecies *parvifolium* is more widely distributed, occurring from northern Hidalgo to Oaxaca and possibly to Guatemala. No geographic pattern is evident in the distribution of the dysploid chromosome races ( $n = 34, 35, 36$ ).



Figures 20-30. Chromosomes of *Sedum* sect. *Pachysedum* at metaphase I in pollen mother cells,  $\times 2000$  (except as indicated). Thin lines point to univalents or B-chromosomes, thicker lines to multivalents. 20, *S. macdougalli*, SSM-SL1,  $n = 34$ ; 21, *S. nussbaumerianum*, C44-93,  $n = 64$ ; 22, *S. pachyphyllum*, U1751,  $n = 34$ ; 23, *S. praealtum* ssp. *praealtum*, O-RB3,  $n = 34$ ; 24-25, *S. praealtum* ssp. *parvifolium*: 24, M7806,  $n = 35$ ; 25, M10074,  $n = 36 + 1B$ ; 26-27, *S. \times rubrotinctum*: 26, UC32.3009, about 10 bivalents (with greater depth of focus) plus about 43 univalents, equivalent to  $2n = 63$ ; 27, UC55.098, pollen, mostly unstained and abortive,  $\times 500$ ; 28, *S. suaveolens*, U2323,  $n = \text{ca. } 320$ ; 29, *S. treleasei*, U1205,  $n = 34$ ; 30, *S. sp.*, UC58.858,  $n = 34 + 1$ .

**Sedum × rubrotinctum.**

*Sedum × rubrotinctum* Clausen is known only in cultivation (Clausen, 1975), and it appears to be a garden hybrid. Meiosis is extremely irregular, and probably most chromosomes are unpaired at metaphase I. About 50–55 elements, including about 10 bivalents and multivalents, were noted in the best cells seen (Figure 26), equivalent to a somatic chromosome number of about 63. Laggards and occasional chromosome bridges are present at anaphase I and more laggards also at anaphase II. Virtually all quartets include extra and/or markedly undersized microspores, and most spores seem to degenerate soon after meiosis. At anthesis only 14 of 1286 pollen grains (1.1%) appeared reasonably normal when stained in aniline blue-lactophenol (Figure 27).

Walther (1931), who incorrectly identified *Sedum rubrotinctum* as *S. guatemalense* Hemsley (Clausen, 1948), noted the “subapical mucros” at the tips of its petals and compared them with similar appendages in *S. stahlii*, which has terminal floral stems. He also commented on other similarities between the two, notably the subshrubby habits and the subterete leaves strongly flushed with bright red. An artificial hybrid, *S. cremnophila* (of sect. *Pachyse-dum*) × *S. stahlii* (Uhl, 1976a) is a good match for *S. rubrotinctum* in most characters, including size, coloring and petal tips, but it has broader, thicker leaves. It seems reasonably certain that *S. stahlii* ( $n = 29$ ) was one parent of *S. rubrotinctum*. The other parent must have been a subshrubby, yellow-flowered *Sedum* with terete leaves, most likely *S. pachyphyllum* ( $n = 34$ , Figure 22). A single seedling resulted from the cross *S. pachyphyllum* (U1751) × *S. stahlii* (M7774) but died before it could be studied. The chromosome number in *S. rubrotinctum* is compatible with this parentage ( $2n =$  ca. 63), and the degree of irregularity in behavior of its chromosomes at meiosis is similar to that seen in artificially produced hybrids between *S. stahlii* and two other species of sect. *Pachyse-dum* (*S. cremnophila* and *S. cuspidatum*, Uhl, 1976a, and unpublished).

**Sedum suaveolens.**

The recently discovered and described *Sedum suaveolens* Kim-nach (1978) has the dubious distinction of having the highest chromosome number yet found in seed plants,  $n = 320$ , or very close

to that (Figure 28). In terms of the basic chromosome number in sect. *Pachyseudum* ( $n = 30-34$ ), this is apparently 20-ploid. Vegetatively this species differs sharply from all other species of sect. *Pachyseudum*, and its sessile rosettes closely resemble those of some species of *Echeveria* (e.g., *E. elegans*) and *Graptopetalum* (e.g., *G. macdougallii*). However, its flowers do not conform to those of *Echeveria* or *Graptopetalum* but seem most similar to those of *S. craigii*, and Kimnach (1978) tentatively assigned it to Clausen's sect. *Craigia*, along with *S. craigii*. Further study may suggest a different classification for this very anomalous species. It is known only from its type locality, near Topia, in northwestern Durango about 230 km. southeast of the locality of *S. craigii*.

#### ***Sedum treleasei*.**

*Sedum treleasei* Rose ( $n = 34$ , Figure 29) is native to southeastern Puebla. All collections studied are of unknown origin in the wild, although one (*U1205*) is traceable back to Rose himself. The collections differ somewhat, with *U1205* having thicker, broader leaves than the others.

#### ***Sedum* sp.**

One collection (*UC58.858*) is clearly an undescribed species ( $n = 34$ ). It has very blue-glaucous, obovate, reddish-tipped leaves up to about 25 mm. long and 8 mm. thick, and vegetatively it somewhat resembles *Sedum pachyphyllum*. However, its petals are pale yellowish and erect in the lower half, then chocolate brown and strongly recurved above. Its only known locality is in the Sierra Madre del Sur of south central Oaxaca, where it was collected by Thomas MacDougall (*B-188*) in 1957. The only plant studied happens to be a trisomic ( $2n + 1$ ), and about half of the metaphase I figures show 34 bivalents and a univalent (Figure 30), and the other half show only 34 elements, presumably including a trivalent.

The floral characters of this species (*UC58.858*) make it difficult to assign it to an existing genus. However, its vegetative characters, its lateral inflorescence, its chromosome number, and especially the pairing behavior of its chromosomes in several hybrids (Uhl, 1976a, and unpublished) clearly favor its assignment to sect. *Pachyseudum*. In particular, a hybrid with *Sedum lucidum* (*U1462* × *UC58.858*) shows nearly normal meiosis, and only bivalent chromosome pairing was noted in about half its cells at metaphase I, with the other cells showing 1-4 univalents and sometimes probably a

multivalent or two. A single chromosome bridge was noted in two cells at anaphase I, but many other cells at this stage appeared normal, and 7.0% stainable pollen is produced. These observations indicate that, in spite of the differences in their flowers, the parental genomes are very similarly organized and probably bear no more than a few small differences in chromosome structure and gene arrangements. Clearly the genes that regulate the morphology and pigmentation of the corolla in the parental species have evolved along different lines, but the overall arrangement and organization of the genes in the parental chromosomes are very much alike. Similar observations also were made for a hybrid with *Echeveria linguifolia* (UC61.583 × UC58.858) (Uhl, 1976a).

#### DISCUSSION

The apparent basic chromosome number in sect. *Pachysedum* ( $n = 30-36$ ) is so high as to suggest that it is polyploid. However, no other evidence supports this conclusion. No similar species with substantially lower chromosome numbers are known that might represent diploid close relatives or ancestors of sect. *Pachysedum*. Species with  $n = 30$  to  $n = 36$  exhibit no tendency to form multivalents at meiosis, as known polyploids in this family generally do (Uhl, 1976a, and unpublished). Strongest evidence for diploidy of these species with  $n = 30-36$  comes from study of many hybrids. Details of this have been published for *Sedum cremnophila* and *Echeveria linguifolia* (Uhl, 1976a). Study of many hybrids involving other species of sect. *Pachysedum* leads to the same conclusion for them also, and for the same reasons: (1) the chromosomes contributed to a hybrid by these species with  $n = 30-36$  are no more potent in determining the phenotype of the hybrid than are other genomes contributing as few as 12 chromosomes, the lowest chromosome number in the comparium; and (2) in the hybrids the chromosomes are unable to pair with other chromosomes from the same parent (autosyndesis), although most of them usually pair successfully with at least some part(s) of one or more chromosomes from the other parent (allosyndesis) (Uhl, unpublished). Both of these properties contrast sharply with the properties of chromosomes from known tetraploids in these groups. If the high basic chromosome numbers here are the result of ancient polyploidy, the original diploid ancestors, if they exist, are no longer apparent, and the genomes

here have now become so thoroughly diploidized that none of the cytological or genetical traits of polyploids, except the high numbers, remain. Similar conclusions have been reached on similar grounds for *Graptopetalum* and *Thompsonella* ( $x = 30-34$  and  $x = 26$ , respectively) (Uhl, 1970) and for *Pachyphytum* ( $x = 31-33$ , Uhl & Moran, 1973).

Although hybrids are easily produced between most species of sect. *Pachyseudum* and subfam. Echeverioideae, attempted crosses between species of sect. *Pachyseudum* and other species of *Sedum* are less likely to result in any progeny. And although very extensive chromosome pairing occurs in most hybrids between sect. *Pachyseudum* and subfam. Echeverioideae, most hybrids between sect. *Pachyseudum* and other species of *Sedum*, when obtained, usually exhibit considerably less chromosome association at meiosis (i.e., they usually have more univalents) (Uhl, 1976a, and unpublished). This observation applies to hybrids of sect. *Pachyseudum* with the relatively large species of *Sedum* with terminal inflorescences (*S. allantoides*, *S. obcordatum*, *S. palmeri*, *S. platyphyllum*, & *S. stahlii*), as well as to hybrids with smaller, more "typical" species of *Sedum*.

Thus, as judged by the extent of their association at meiosis, the chromosomes of sect. *Pachyseudum* of *Sedum* are more closely homologous with the chromosomes of most species of subfam. Echeverioideae than they are with most or all other species of *Sedum*. Since the ability of chromosomes to synapse at meiosis is a strong indicator of their homology and genetic similarity, sect. *Pachyseudum* seems to be significantly closer genetically to subfam. Echeverioideae than it is to the rest of *Sedum*.

The genera of subfam. Echeverioideae appear to have ancestral chromosome numbers in the range of 30-35 (Uhl, 1970, 1976a, and unpublished; Uhl & Moran, 1973), the same as in sect. *Pachyseudum*. The latter appear to be an intermediate group between typical *Sedum* and subfam. Echeverioideae, and they may resemble the ancestral stocks from which the latter were derived. Walther (1931) stressed the close resemblance between *Sedum cremnophila* and *Echeveria linguifolia* and suggested that "possibly the transition between *Echeveria* and the more primitive genus *Sedum* may be sought in this vicinity". The evidence from the chromosome numbers, presented here, and the evidence from study of many hybrids, to be presented elsewhere, support this idea.

Traditionally classification of the Mexican Crassulaceae into subfamilies and genera has been based chiefly upon characters of the corolla, especially its attitude and connation. However, the cytological evidence indicates that corolla characters are of limited taxonomic value here, since parallel conditions appear to have evolved independently several times in related lines. Some taxonomic revision seems appropriate to bring the classification of sect. *Pachysedum* into closer harmony with its natural relationships. One possible improvement might be to expand the recently revived *Cremnophila* (Moran, 1978) to include most or all species of *Pachysedum* (and probably also several species of *Echeveria*) and to assign the genus to subfam. Echeverioideae.

**Table 1. Chromosome Numbers in Sedum Section Pachysedum**

***Sedum adolphii* Hamet  $n = 64$**

*U1938*, *UC62.241*, *C45-97* (Figure 1), *C46-32* All cultivated.

***Sedum* × *amecamecanum* Praeger Meiosis irregular.**

*U483* (Figures 2, 3, 5) Cultivated.

*M7800* (Figure 4) Cultivated in Mexico. Said to have come from 3000 m. on Popocatepetl.

***Sedum batallae* Barocio  $n = 34$**

*M13411* (Figure 6) Topotype. Hidalgo: sheer cliffs of Cerro Alto, 2½ km. S. of Epazoyucan, 2600 m. (R. Moran, C. H. Uhl, & H. Sanchez-Mejorada).

***Sedum clavatum* Clausen  $n = 33$**

*TMV-T-Tis. 1* & *Tis. 3* (Figure 7) State of Mexico: Tiscalatengo Gorge, 4 km. WSW of Tenancingo (R. T. Clausen) Type Collection.

*M19058* (Figure 8) Same locality (H. Fittkau)  $n = 33 + 1B$ .

*U1566* (Figure 9) Same locality (J. Meyran 1306)  $n = 33 + 2B$ .

***Sedum confusum* Hemsley  $n = 34$**

*C44-14* (Figure 10), *C46-14*, *UC45.323* All cultivated.

***Sedum corynephyllum* Fröderström  $n = 34$**

*M13386* San Luis Potosi: Sierra La Aquitaria, 34 km. SW of Rioverde (R. Moran & C. H. Uhl).

*U2339* Hidalgo: Palo Hueco, 28 km. NE of Jacala, 1700 m.

*U2127* Queretaro: 24 km. NE of Vizarron.

*M10042*, *M10047* Hidalgo: Barranca de Toliman (R. Moran).

*C48-55* Hidalgo: near Zimapan (R. T. Clausen).

*M7802*, *U258* (Figure 11), *C47-71* All cultivated.

***Sedum corynephyllum*** Fröderström  $n = 68$

*U1286* Hidalgo: 7 km. N. of Metzquititlan (M. Kimnach).

*M7796* (Figure 12) Same or nearby locality (R. Moran).

*UC57.577* Hidalgo: Barranca de Venados (P. C. Hutchison).

***Sedum craigii*** Clausen  $n = 30$

*C43-2* (Figure 13) Isotype. Chihuahua: Canyon wall of Barranca del Cobre 2135 m. (R. T. Craig & G. Lindsay).

*U1206*. Cultivated. Probably same collection.

***Sedum cremnophila*** Clausen  $n = 33$

*M10174* (Figure 14) Tep 2, Tep 3, Tep 6 ( $n = 33 + 1B$ ), Tep 7 Morelos: above Aztec temple, N. of Tepoztlan (R. Moran, R. T. Clausen).

*U1291*, *U1435*, *M7687* Morelos: Sierra de Chalchi, S. of Tepoztlan, on cliffs (M. Kimnach, C. H. Uhl, & R. Moran).

***Sedum cuspidatum*** E. J. Alexander  $n = 34$

*U1263* (Figure 15) Oaxaca: Sierra Madre above Zanatepec (T. MacDougall, *B-236*).

*C46-62* Clonotype. Chiapas: near Ocozocoautla (T. MacDougall).

*C49-25* Chiapas: WSW of Tuxtla Gutierrez.

*UC52.1881* Cultivated (Coll. by T. MacDougall).

***Sedum decumbens*** Clausen  $n = 34$

*C44-119* Cultivated. Type collection.

***Sedum dendroideum*** Moc. & Sesse  $n = 30$

*M7785* Hidalgo: Pachuca (R. Moran).

*M7779* (Figure 16) Puebla: San Hipolito (R. Moran).

*SJC* Oaxaca: San Jose Chiltepec (T. MacDougall).

*M7736* Oaxaca: Cañada de Tutla (R. Moran).

*UC56.799* Oaxaca: Cerro Atravesado, Juchitan (T. MacDougall, *B-176*).

**Sedum hultenii** Fröderström  $n = 26$ 

*U1864* Hidalgo: 8 km. S. of Santa Ana, 1600 m.

*U1865* Hidalgo: 10 km. S. of Santa Ana, 1600 m.

*U1937* Hidalgo: Cantil de Tambor, 11 km. S. of Santa Ana, 1650 m.

*U1868* Hidalgo: 23 km. N. of Jacala.

*C7472* (Figure 17) Puebla: Near Huauchinango (Topotype?) (R. T. Clausen).

*U2349* Puebla: 2 km. W. of dam at Nuevo Necaxa, 1600 m.

*U1881* Puebla: 8 km. N. of Zacapoaxtla, 1375 m.

*U485* Cultivated: Uppsala, Sweden. Likely from the type collection.

*M14783* Cultivated. Said to be from Hidalgo (H. Fittkau).

**Sedum lucidum** R. T. Clausen  $n = 34$ 

*C44-12* (Figure 18) Type collection. Veracruz: Orizaba (E. Walther).

*RB6* 5 km. SW of Orizaba city (R. T. Clausen).

*U1462* Veracruz: E. of town of Rio Blanco.

*M3179*, *C48-24*, *C49-13* All cultivated.

**Sedum** × **luteoviride** R. T. Clausen Meiosis irregular.

*M7808* Hidalgo: Near San Vicente, ca. 35 km. S. of Jacala, 2300 m. (R. Moran).

*C47-76*, *M7616*, *M7801* (Figure 19) All cultivated.

**Sedum macdougallii** Moran  $n = 34$ 

*SSM = SL1* (Figure 20) Topotype. Oaxaca: Santiago Lachiguiri. (T. MacDougall).

**Sedum nussbaumerianum** Bitter  $n = 64$ 

*C44-93* (Figure 21), *C46-27* Both cultivated (R. T. Clausen).

**Sedum pachyphyllum** Rose  $n = 34$ 

*U191*, *U1751* (Figure 22), *FL1420* All cultivated.

**Sedum praealtum** DC ssp. **praealtum**  $n = 34$ 

*U1887* Veracruz: S. side of valley opposite city of Rio Blanco.

*RB3* (Figure 23) Same or nearby locality (R. T. Clausen).

**Sedum praealtum** DC ssp. **parvifolium** Clausen  $n = 34$ 

*U1468* Hidalgo: 3.6 km. N. of Pueblo Nuevo.

*C7437* Hidalgo: Rocks by waterfall near Pueblo Nuevo, 3050 m. (R. T. Clausen).

*C7430* Hidalgo: Rocks beside road, Real del Monte, 2745 m. (R. T. Clausen).

*C7533* Hidalgo: Barranca de los Marmoles, 37 km. N. of Zimapan, 2300 m. (R. T. Clausen).

*M-M* Tlaxcala: NE side of Malinche (5 plants) (R. T. Clausen).

*M7770* Oaxaca: Las Flores, Sierra Juarez (R. Moran).

*M10130* Oaxaca: Cerro San Felipe (R. Moran).

*SSM-SL1* Oaxaca: San Luis (R. T. Clausen).

*U842* Guatemala: Dept. El Quiche. Chichicastenango, possibly cultivated (H. E. Moore, Jr.).

***Sedum praealtum* DC ssp. *parvifolium* Clausen  $n = 35$**

*M7806* (Figure 24) Hidalgo: San Vicente, ca. 35 km. S. of Jacala, 2300 m. (R. Moran).

*U1882* Puebla: E. of Teziutlan.

*U1461* Veracruz: 1 km. NE of Cumbres de Acultzingo.

*UC58.842* Oaxaca: below Neveria, Santo Domingo Ozolotepec, 2600 m. (T. MacDougall, *B-189*).

***Sedum praealtum* DC ssp. *parvifolium* Clausen  $n = 36 + 1B$**

*M10074* (Figure 25) Hidalgo: El Carmen (R. Moran).

***Sedum* × *rubrotinctum* Clausen Meiosis irregular**

*M3090*, *UC32.3009* (Figure 26), *UC55.098* (Figure 27) All cultivated.

***Sedum suaveolens* Kimnach  $n = 320 \pm$**

*U2323* (Figure 28) Type collection. Durango: vertical cliff face in river canyon 3 km S. of Topia. *M. Kimnach & H. Sanchez-Mejorada 1784*.

***Sedum treleasei* Rose  $n = 34$**

*U1205* (Figure 29) Cultivated, Univ. of Mich. Bot. Garden 9375, from J. N. Rose in 1921.

*U475*, *U2444* Cultivated.

***Sedum* sp.  $n = 34 + 1$**

*UC58.858* (Figure 30) Oaxaca: Below Neveria, Santo Domingo Ozolotepec, 2600 m. (T. MacDougall, *B-188*).

## SUMMARY

Section *Pachysedum* is defined as consisting of 19 Mexican species having lateral floral stems and mostly shrubby or subshrubby habit and *Sedum*-like flowers. Chromosome numbers are reported for 82 collections representing all 19 species: one species has  $n = 26$ , two each have  $n = 30$  and  $n = 33$ , 11 have  $n = 34$ , two have  $n = 64$ , and one has  $n = 320 \pm$ , probably 20-ploid and the highest known in seed plants. One species includes diploid and tetraploid populations ( $n = 34, 68$ ); another has populations with 3 different dysploid numbers ( $n = 34, 35, 36$ ); one trisomic was noted; and B-chromosomes were found in 3 species. Chromosome numbers are also reported here for three other named species which have very irregular meiosis and appear to be sterile; they are believed to be natural or garden hybrids each having a species of sect. *Pachysedum* as one parent. In many artificial hybrids the very extensive homology and pairing between chromosomes of different species of sect. *Pachysedum* supports the conclusion that most or all of them represent a natural group. In spite of their relatively high numbers, the 30–34 gametic chromosomes contributed by most species of sect. *Pachysedum* do not pair among themselves in hybrids, and such species are considered effectively diploid. Substantial chromosome pairing occurs in hybrids between species of sect. *Pachysedum* and subfam. Echeverioideae, whereas considerably less chromosome pairing occurs in most hybrids between species of sect. *Pachysedum* and other Mexican species of *Sedum* that have terminal floral stems. This indicates that sect. *Pachysedum* is more closely related genetically to subfam. Echeverioideae than it is to most or all other species of Mexican *Sedum*. Some taxonomic realignment seems desirable here to bring the classification into closer agreement with the genetic relationships.

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